

# THE SUPPOSED NYMPHS OF THE PALÆODICTYOPTERA<sup>1</sup>

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Our knowledge of the metamorphosis of Carboniferous insects is meager. Inferences have been made about their immature stages, but actual knowledge is restricted to the fossils which have been found. Furthermore, although some Carboniferous nymphs are known, it is difficult to associate them with adults. Specific association is obviously impossible; the best that can be done is association by family or order. If the fossils concerned are members of an existing order, the association can be made with near certainty, for the living immature and imaginal forms provide a basis for comparison; but if the fossils are adults belonging to an extinct order, the problem of identifying their immature stages is more difficult. This is well illustrated by the nymphs which have been referred to the extinct order Palæodictyoptera, and which have been extensively discussed in the literature on wing development. Speculation about these nymphs and their significance has been so great that I have thought it worth-while to summarize here what is actually known about them.

Five palæodictyopterous nymphs have been described up to the present time, four by Handlirsch (1906) and one by Goldenberg (1873). All are from Carboniferous strata. Through the courtesy of Dr. R. S. Bassler and Dr. G. A. Cooper, I have been able to examine the four Handlirsch specimens in the United States National Museum. I have not seen the Goldenberg fossil, which is in the collection of the Natural History Society at Bonn, Germany, but it has been redescribed and figured by v. Schlechtendal (1913) and Guthörl (1934). Handlirsch placed all these species in the "form genus" *Palæodictyopteron*, but he also used that term as a generic name

<sup>1</sup> Published with a grant from the Museum of Comparative Zoölogy at Harvard College.

for adult Palæodictyoptera with obscure family relationships. Since, for reasons given below, I consider their ordinal position obscure, I have assigned these nymphs to *Insecta Incertæ Sedis*.

*Insectorum* gen. indet. *anglicanum* Handl.

Plate 6, figures 1 and 5; plate 7, figure 1.

(*Palæodictyopteron*) *anglicanum* Handlirsch, 1906, Foss. Ins.: 52, pl. 8, fig. 16.

The specimen on which this species is based is preserved in an ironstone nodule, from Sedgley, England, and is now in the U. S. National Museum (Type no. 38109, Beale Collection). Handlirsch's figure of the fossil, which is reproduced here (plate 6, figure 1) depicts a slender wing or wing-pad, a fragment of another, parts of the head (including one compound eye), thorax and abdomen. The wing-pad is shown extending laterally from the thorax, its longitudinal axis being perpendicular to the longitudinal axis of the thorax. This figure has been referred to several times in entomological literature and has caused much speculation about the development of the Palæodictyoptera. Comstock, in his "Wings of Insects" (1918), refutes Handlirsch's contention that immature Palæodictyoptera were aquatic by pointing out that it would be "difficult to imagine insects with laterally projecting wing buds, such as these nymphs possessed, swimming through the water." Lemche (1940) uses the same figure as a source of important evidence to aid his theory of polyphylectic origin of wings in insects. Similarly, Forbes (1943) has employed it to support his erection of an extinct order, *Anasaxia*. The Palæodictyoptera differed from the *Anasaxia*, in part, by having nymphs "with the wing-pads extending directly out, unlike all other insects."

The fossil responsible for all this speculation is poorly preserved, as shown in the accompanying photograph (plate 7, figure 1). So far as I have been able to determine, it consists only of a single wing or wing-pad and suggestions of the abdomen (plate 6, figure 5). The thorax and head are not discernible and the object which

Handlirsch identified as an eye is plant material, like that covering most of the nodule. There is therefore no evidence whatever that the wing-pads of this insect were developed perpendicularly to the thorax. The wing itself, however, shows more details than are indicated in Handlirsch's figure or description. It is about 7 mm. long, with an anterior margin that is slightly concave proximally and convex near the middle. The most obvious feature of the wing is a prominent longitudinal ridge (or groove, in the counterpart), which is probably the radius (R1). Between it and the anterior margin is a weaker interrupted ridge, and posterior to it is what appears to be a forked vein. There is also a suggestion of a posterior submarginal vein.

The part of the abdomen that is preserved consists of five or six broad segments. These few segments indicate an abdomen that is large in proportion to the wing,—a peculiarity suggesting that the insect was a nymph. This was probably the case, but there is another possibility worth mentioning: the wing of the fossil is much like the elytron of some Protelytroptera, even to the concave anterior margin, the heavy R1, and the posterior, submarginal vein. Without more precise knowledge of the fore wing and at least part of the hind wing, we can reach no conclusion on the ordinal position of this fossil. There is certainly nothing to show that it is palaeodictyopterous, and Handlirsch, although describing the specimen as a nymph of that order, gave no reason for his conclusion.

*Insectorum* gen. indet. *virginianum* Handl.

Plate 6, figure 2; plate 7, figure 2.

(*Palaeodictyopteron*) *virginianum* Handlirsch, 1906, Foss.

Ins.: 63, pl. 8, fig. 19; 1906, Proc. U. S. Nat. Mus., 29: 689, fig. 16.

The type of this species is preserved in black shale, from soft coal beds near Redbird, West Virginia, and is now in the National Museum (No. 25635). Handlirsch's drawing of the fossil is reproduced here (plate 6, figure

2); it depicts a basal piece of the fore wing-pad, a complete hind wing or its bud, and fragments of the thorax and abdomen. As in the case of the preceding species, the figure shows the wings extending laterally from the thorax, and it was reproduced by Comstock (1918, fig. 81) to demonstrate the lateral formation of wings in palæodictyopterous nymphs.

Examination of the fossil convinces me that Handlirsch, in making his drawing, confused plant remains with those of the insect, as can be seen from the accompanying photograph (plate 7, figure 2). The fragment of the fore wing represented in his figure is either a piece of a plant or of the insect's body; it is clearly not a wing or wing-bud, and it bears a relationship to the true wing different from that shown in his figure. The parts of the "thorax" and "abdomen" are clearly of plant origin. The wing itself is about 10 mm. long, and much more oval than shown in Handlirsch's figure. There are faint indications of veins or ridges, but they cannot be followed satisfactorily because of numerous wrinkles. Although this wing is very different from that of the foregoing insect in shape, size and texture, there is no evidence that it was either palæodictyopterous or a nymphal structure.

*Insectorum* gen. indet. *mazonum* Handl.  
Plate 6, figure 3.

(*Palæodictyopteron*) *mazonum* Handlirsch, 1906, Foss. Ins.: 63, pl. 8, fig. 17; 1906, Proc. U. S. Nat. Mus., 29: 688, fig. 14.

This is preserved in an ironstone nodule, from the vicinity of Morris, Illinois (Type no. 38831, U. S. National Museum). Handlirsch's figure is correct in depicting the distal part of a wing, 18 mm. long, which could be either nymphal or mature. The apparent thickness of the fossil suggests that it is a wing-pad, possibly of a roach or Protorthopteron. Its assignment to the Palæodictyoptera is entirely without foundation and Handlirsch gave no reason for placing it there.

*Insectorum* gen. indet. *latipenne* Handl.  
Plate 6, figure 6.

(*Palæodictyopteron*) *latipenne* Handlirsch, 1906, Foss. Ins.: 63, pl. 8, fig. 18; 1906, Proc. U. S. Nat. Mus., 29; 688, fig. 15.

This is also preserved in an ironstone nodule of the Carbondale Formation, from near Braidwood, Illinois (Type no. 38838, U. S. National Museum). As Handlirsch shows, it consists of a poorly preserved wing, 22 mm. long, with a distinctly enlarged anal area. There is no sign of the body and the only suggestion that the fossil is a nymphal wing lies in its apparent thickness. There is nothing, however, to show that it is palæodictyopterous; it could have belonged as well to a nymph of a Protorthopteron or a related Carboniferous order.

*Insectorum* gen. indet. *hageni* Gold.  
Plate 6, figure 4.

*Termes hageni* Goldenberg, 1873, Fauna saræp. foss., 1: 12; pl. 2, fig. 7b.

(*Palæodictyopteron*) *hageni* Handlirsch, 1906, Foss. Ins.: 62, pl. 8, fig. 15; v. Schlectendal, 1913, Nova Acta Leop., 98: 99, pl. 1, fig. 7; pl. 8, fig. 1.

(*Dictyoneuridæ*) *hageni* Guthörl, 1934, Preuss. Geol. Landes., 164: 84, fig. 48; pl. 13, fig. 6.

This fossil, from the Saarbrücken beds of Germany, was originally thought by Goldenberg to be a wing of a termite. It has subsequently been examined and described by Handlirsch, v. Schlectendal, and Guthörl, who have considered it a palæodictyopterous wing-pad. The discrepancy in the figures of the three last workers is astonishing. Handlirsch shows a complete wing, with entire margins; v. Schlectendal, a wing fragment, the wing being broken posteriorly and distally; Guthörl, a wing fragment with all margins broken. Guthörl's and v. Schlectendal's figures are alike in venation, but differ markedly from Handlirsch's. From these and the photograph reproduced by Guthörl, the fossil appears to be a proximal fragment (9 mm. long) of a small wing, pos-

sibly a wing-pad; but there is nothing to show its affinities.

From the foregoing account I believe it is clear that none of the fossils described as palæodictyopterous nymphs can rightly be so considered until further evidence is at hand. Consequently, we have no actual record of the nymphs of these insects and no knowledge whatever of their wing development. It is noteworthy, in this connection, that nymphs of the related order Megasecoptera have been described by Handlirsch (1911), from Illinois, and Bolton (1921) from England. Those studied by Bolton show a venational pattern strongly resembling that of the adult insects of the family Brodiidæ, and since both adults and nymphs occur in the same deposit, their association seems justified. Handlirsch's (*Palæodictyopteron*) *anglicanum*, which has been discussed above, may be a poorly preserved and distorted specimen of this type. His megasecopterous nymph, from the vicinity of Mazon Creek, is so much like Bolton's that its assignment to the Megasecoptera is highly probable. At any rate, none of these nymphs, which, incidentally, show the usual type of wing development, can be referred to the Palæodictyoptera. For the present, therefore, we remain in complete ignorance of their immature stages.

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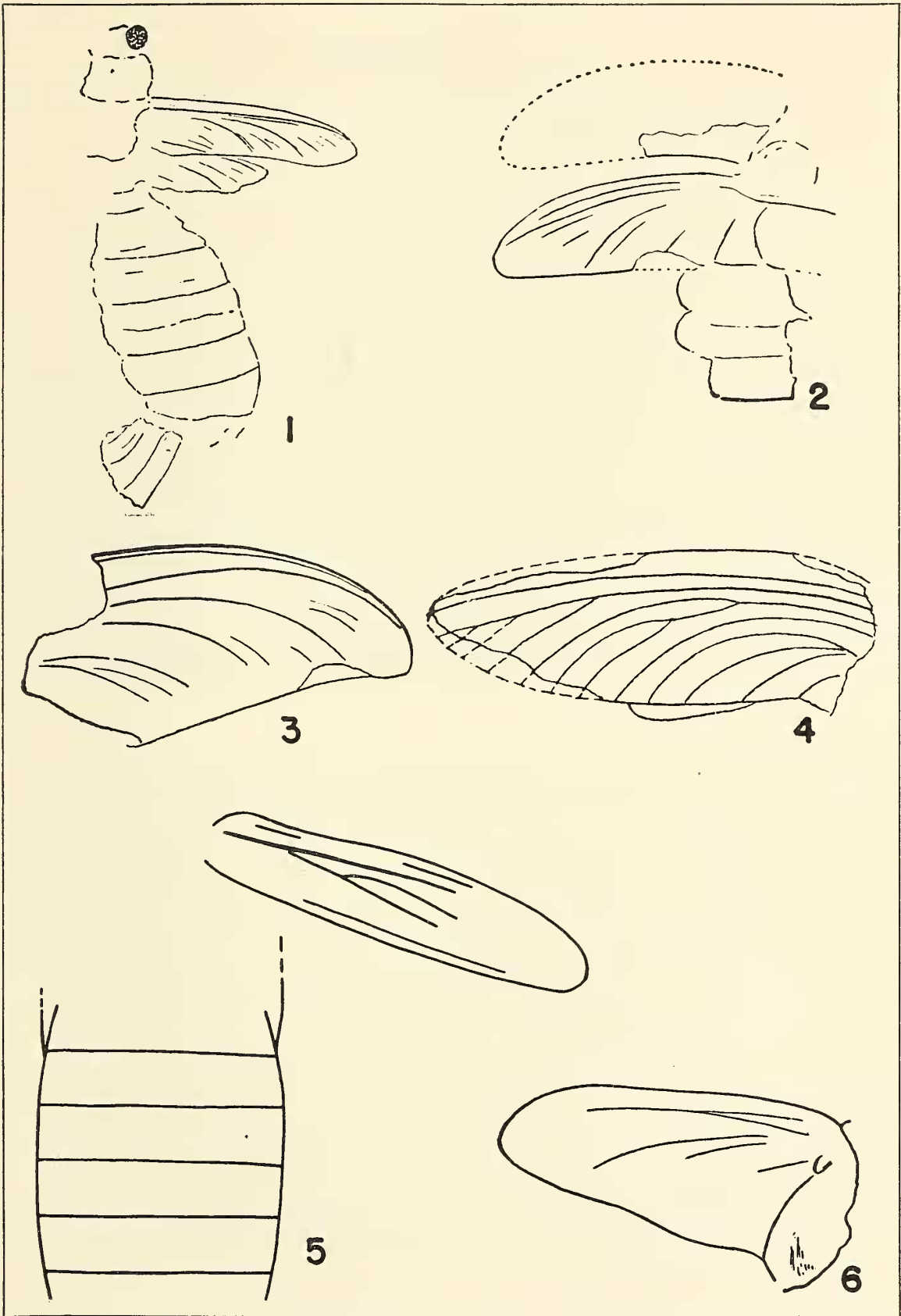
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## EXPLANATION OF PLATE 6

- Fig. 1. *Insectorum* gen. indet. *anglicanum* Handl. From Handlirsch, 1906.  
Fig. 2. *Insectorum* gen. indet. *virginianum* Handl. From Handlirsch, 1906.  
Fig. 3. *Insectorum* gen. indet. *mazonum* Handl. From Handlirsch, 1906.  
Fig. 4. *Insectorum* gen. indet. *hageni* Gold. From Guthörl, 1934.  
Fig. 5. *Insectorum* gen. indet. *anglicanum* Handl. Original drawing,  
based upon type.  
Fig. 6. *Insectorum* gen. indet. *latipenne* Handl. From Handlirsch, 1906.





CARPENTER—PALAEDICTYOPTEROUS NYMPHS

## EXPLANATION OF PLATE 7

- Fig. 1. Photograph of the type of *Insectorum* gen. indet. *anglicanum*  
Handl. (U. S. Nat. Museum, no. 38109).
- Fig. 2. Photograph of the type of *Insectorum* gen. indet. *virginianum*  
Handl. (U. S. Nat. Museum, no. 25635).